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12 Neoteny and the Plesiomorphic Condition of the Plesiosaur Basicranium

F. Robin O'Keefe

Introduction

Historically, the systematics of the Plesiosauria (Reptilia, Sauropterygia) were based largely on postcranial characters (Persson, 1963; Brown, 1981). Several factors account for this bias: plesiosaur skulls tend to be delicate and are often crushed even when preserved, postcranial elements are relatively common and cranial elements are not, lack of knowledge about the relationships of stem-group sauropterygians, and lack of knowledge of plesiosaur cranial anatomy itself. However, recent detailed examinations of plesiosaur cranial anatomy have identified many characters of use in plesiosaur systematics (Brown, 1993; Cruickshank, 1994; Storrs & Taylor, 1996; Storrs, 1997; Carpenter, 1997; Evans, 1999; O'Keefe, 2001, 2004), and the systematics of the group have changed markedly in response (Carpenter, 1997; O'Keefe, 2001, 2004). The work of Rieppel and others has clarified the anatomy and relationships of stem-group sauropterygians (Storrs, 1991; see Rieppel, 2000, for review). This work has laid the anatomic and phylogenetic foundations for a better understanding of plesiosaur cranial anatomy.

The purpose of this paper is to describe the condition of the braincase in stratigraphically early and morphologically primitive plesiosaurs. Information on the braincase of plesiomorphic taxa is important because it establishes the polarity of characters occurring in more derived plesiosaurs. This paper begins with a short review of braincase anatomy in stem-group sauropterygians. Data on braincase morphology of the plesiomorphic plesiosaur genera *Thalassiodracon* and *Eurycleidus* are then presented and interpreted via comparison with other plesiosaurs, stem-group sauropterygians, and stem diapsids (*Araeoscelis*). Early diapsids are relevant because plesiosaur skulls more closely resemble early diapsids than stem-group sauropterygians in several key areas. Plesiosaurs display a broad trend of delayed and reduced ossification compared with stem-group sauropterygians (Storrs, 1991). This trend is linked to the acquisition of a truly pelagic lifestyle in the Plesiosauria (Romer, 1956).

As pointed out by Rieppel (2000, 113), plesiosaurs show several reversals to plesiomorphic character states, such as the reappearance of posterior interpterygoid vacuities. This paper advances the hypothesis that reversal in this and several other cranial characters is a consequence of heterochrony, specifically neoteny in the ossification of the pterygoid (Gould, 1977).

The Braincase in Stem-Group Sauropterygians

One barrier to understanding the plesiosaur braincase is the condition of the basicranium in stem-group sauropterygians. All "nothosaur"-grade taxa (i.e., all Sauropterygia exclusive of clade Pistosauria; see fig. 12.7) lack interpterygoid vacuities in the posterior palate; the pterygoids meet in an unbroken median suture running from the vomers anteriorly and caudad to the occipital condyle and therefore hide the basicranium in ventral view (Rieppel, 1994). In plesiosaurs, the palate is quite different. Posterior interpterygoid vacuities are present, as in early diapsids, and an anterior interpterygoid vacuity sometimes allows a view of the relations of the anterior end of the parasphenoid (O'Keefe, 2001).

The braincase in plesiosaurs is an open and poorly ossified structure, and different patterns of ossification are taxonomically informative (O'Keefe, 2001). The occiput is closed and plate-like in many nothosaur-grade taxa, further obscuring the more anterior relationships of braincase elements; however, Rieppel used well-preserved material to produce detailed reconstructions of the braincase in *Simosaurus, Nothosaurus* (Rieppel, 1994), and *Cymatosaurus* (Rieppel & Werneburg, 1998). *Simosaurus* and *Nothosaurus* are nothosauroids possessing a closed occiput, while *Cymatosaurus* is a pistosauroid possessing an open occiput very similar to that found in all plesiosaurs (Rieppel, 2000). The closed occiput of nothosauroids is characterized by large and plate-like exoccipitals and opisthotics with a clear suture between the two elements, whereas more laterally the opisthotic possesses a long dorsolateral suture with the descending occipital flange of the squamosal (Rieppel, 1994). The posttemporal fossa in both taxa is reduced to a small foramen. Below the ventral margin of the exoccipital and opisthotic, the cranioquadrate passage lies partially open in *Simosaurus,* whereas in *Nothosaurus* the pterygoid meets the opisthotic in a long transverse suture, closing off the cranioquadrate passage.

The closed nature of the occiput leaves several identifiable foramina for the passage of structures into and out of the head; most prominent is the foramen magnum, on either side of which rest the pillar-like bodies

of the exoccipitals. Just lateral to these pillars and still within the exoccipitals are the jugular foramina. Lateral and slightly ventral to this position are foramina in the pterygoid for the passage of the internal carotid. Lastly, two foramina in the ventromedial aspect of each exoccipital pillar allow passage for the hypoglossal nerve (Rieppel, 1994); plesiosaurs usually have two foramina in the same position for the hypoglossal nerve (Hopson, 1979; Storrs & Taylor, 1996; Carpenter, 1997; Evans, 1999). Evans (1999) illustrates a single foramen in *Muraenosaurus.*

In contrast to the closed occiput in nothosauroids, the occiput is open in the pistosauroids *Corosaurus* and *Cymatosaurus* as well as in all pistosaurians including plesiosaurs. The occiput in all plesiosaurs is broadly open, possessing a large posttemporal fenestra bounded dorsally by the squamosal arch and ventrally by the slender paroccipital process (Williston, 1903, 26; Storrs & Taylor, 1996; Carpenter, 1997). The paroccipital process is formed by the opisthotic. The exoccipital is reduced to a column forming the boundary of the foramen magnum. The paroccipital process articulates laterally with the median surface of the squamosal in most plesiosaur taxa (O'Keefe, 2001). Below the paroccipital process is a large cranioquadrate passage bordered by the quadrate, squamosal, pterygoid, basioccipital, and exoccipital/opisthotic (Storrs and Taylor, 1996).

Rieppel described the unusual course of the internal carotid from the occiput to the brain in both *Nothosaurus* (Rieppel, 1994) and *Cymatosaurus* (Rieppel & Werneburg, 1998). In both taxa, the internal carotid travels anteriorly from the occiput within a prominent groove in the dorsal surface of the quadrate ramus of the pterygoid until reaching the basisphenoid and then courses ventrally between the lateral aspect of the basisphenoid and prootic before dividing into the palatine artery and the cerebral carotid (Rieppel, 1994). This course of the internal carotid—characterized by a groove in the dorsal aspect of the pterygoid—is an apomorphy of the Eusauropterygia, although the course of this vessel is currently unknown in pachypleurosaurs and placodonts (Rieppel, 2000). This character is reversed in most plesiosaurs (see below).

In nothosauroids, the cerebral carotid enters the base of the sella turcica ventrolaterally through two prominent foramina separated by a low ridge of bone (Hopson, 1979; Rieppel, 1994). This ridge of bone runs anteriorly along the median dorsal aspect of the palate and is probably the root of a cartilaginous interorbital septum (Romer 1956, 57) extending back into the hypophyseal fossa and subdividing that structure, as noted by Hopson (1979, 120). An identical condition exists in the pistosauroid *Cymatosaurus* (Rieppel & Werneburg, 1998) and in the

plesiosaur *Thalassiodracon* (see below). Last, the basal articulation between ossifications of the palatoquadrate cartilage and the lateral braincase wall is "obliterated" in all stem-group sauropterygians, yielding an akinetic skull (Rieppel, 1994, 2000). The pterygoid encloses the basicranium in these taxa, and a discreet basal articulation is obscured by the extensive contact between pterygoid and basicranium in general. In plesiosaurs, this character is also reversed; a discreet and well-developed basal articulation is present in many taxa (O'Keefe, 2001), although it does not always ossify in later pliosaurids.

The pattern of the semicircular canals is currently unknown in basal sauropterygians. Because of the general reduction of ossification in the endochondral elements of the plesiosaur braincase, however, the paths of the three semicircular canals and the locations of the anterior and posterior ampullae have been identified in several plesiosaur genera (*Peloneustes,* Andrews, 1913; *Cryptoclidus,* Brown, 1981; *Eurycleidus,* Cruickshank, 1994; *Libonectes* and *Dolichorhynchops,* Carpenter, 1997; *Muraenosaurus,* Evans, 1999). All these genera show a similar condition. The posterior ampulla is located in the body of the fused exoccipital/opisthotic, and this bone contains a deep fossa, open anteromedially, for this structure. The horizontal semicircular canal leaves the posterior ampulla laterally and passes directly into the posterior edge of the prootic through the suture between this bone and the exoccipital/opisthotic. The anterior ampulla is located in the prootic, where it resides in a shallow, medially open fossa. The anterior ampulla accepts the horizontal semicircular canal posteriorly, and the canal in the prootic for the anterior portion of this canal is either open or roofed depending on the degree of ossification of the prootic. The posterior vertical semicircular canal ascends through the body of the exoccipital and enters the supraoccipital, where it communicates with the superior utriculus. The anterior vertical semicircular canal leaves the superior utriculus and descends into the prootic, passing through the suture between prootic and supraoccipital. Again, the groove of the anterior vertical semicircular in the prootic can be open or closed depending on the degree of ossification.

In summary, the internal ear in plesiosaurs is not derived and is similar to the condition illustrated in *Captorhinus* by Price (1935). The posterior ampulla resides in the fused exoccipital/opisthotic, and the suture between these two bones is seldom apparent in plesiosaurs. However, Andrews (1913) illustrated a specimen of *Peloneustes* that does preserve this suture. On the medial wall of the foramen magnum, the suture between opisthotic and exoccipital angles from anteroventral to posterodorsal; the jugular

foramen is a gap within this suture as is expected given its developmental origin within the metotic fissure (de Beer, 1937). The paroccipital process is formed entirely of opisthotic, and the fossa for the posterior ampulla is contained within the opisthotic, again like *Captorhinus* (Price, 1935). Below I refer to the fused exoccipital/opisthotic as simply the "exoccipital" except in cases in which the suture between the two elements is clear.

Materials and Methods

This study utilizes material from the Permian diapsid *Araeoscelis* as well as the Early Jurassic plesiosaur taxa *Thalassiodracon, Eurycleidus,* and *Plesiopterys.* Material examined is listed by taxon below.

Institutional abbreviations are as follows: FMNH, Field Museum of Natural History, Chicago; OXFUM, Geological Collections, University Museum, Oxford, UK; CAMSM, Sedgwick Museum, Cambridge, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Material

Araeoscelis casei. The partial skull figured here (fig. 12.1) is specimen number FMNH UR 2419. The skull is small and may represent a juvenile. At this time members of the genus *Araeoscelis* are assigned to two

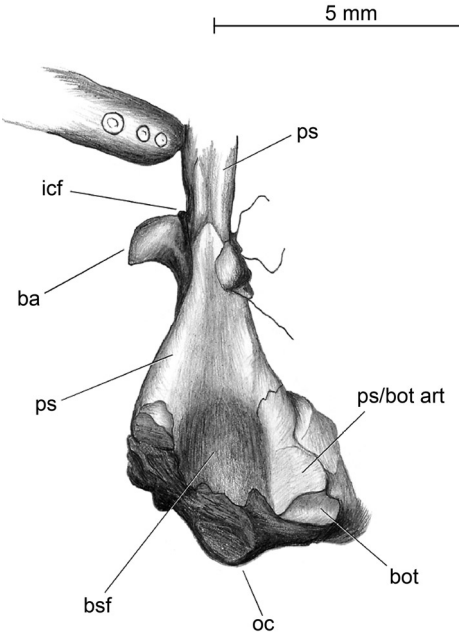

Figure 12.1. Basicranium of a juvenile specimen of *Araeoscelis casei,* FMNH UR 2419. Abbreviations: art, articulation; ba, basal articulation; bot, basioccipital tuber; bsf, basisphenoid fossa; icf, internal carotid foramen; oc, occipital condyle; ps, parasphenoid.

species based mainly on stratigraphic position, although the species are very similar and the genus usually is treated as one form (Vaughn, 1955; Reisz et al., 1984). *Araeoscelis* occurs in three localities in central Texas, two of which are in the Wichita Group; the remaining locality is in the Clear Forks Group (Lower Permian; see Reisz et al., 1984 for details). The skull figured in this paper is poorly preserved except for the basicranium.

Thalassiodracon hawkinsi. This plesiosaur taxon is known from several specimens originating from one locality, the lowermost Lias (Rhaetian/Hettangian) of Street, Somerset, United Kingdom (see Storrs & Taylor, 1996, for a thorough review of this taxon). This genus is one of the stratigraphically earliest plesiosaurs for which adequate material is known and is correspondingly plesiomorphic, sharing several symplesiomorphies with pistosaurids that are lost in later plesiosaurs, including low neural spine height, an angled humerus, presence of nasals, and the presence of a posterior postorbital process (O'Keefe, 2001). The present study deals with the skull figured and described in detail by Storrs and Taylor (1996; CAMSM J.46986). Reference is also made to a skull in the University Museum of Oxford, OXFUM J.10337.

Eurycleidus arcuatus. This taxon was redescribed by Cruickshank (1994) following the extensive preparation of a historical specimen first dealt with by Owen (1840). The specimen resides in the University Museum of Oxford (OXFUM J.28585) and is a fragmentary but well-preserved skull with accompanying postcranial material. The provenance of the material is somewhat unclear, with the only sure information being the source of the fossil, which is "Lower Lias, Lyme Regis." Cruickshank (1994) considered the most likely age to be Hettangian-Lower Sinemurian, although the Pliensbachian is also possible.

Plesiopterys wildi. This taxon was named by O'Keefe (2004) and is a morphologically primitive plesiosaur from the Posidonienschiefer near Holzmaden, Germany. It is of Lower Toarcian age. The holotype of this taxon is a complete skeleton with a crushed and disarticulated skull (SMNS 16812); elements of the braincase are extremely well preserved and are illustrated here. This material was originally referred to *Eurycleidus* by O'Keefe (2001), but further research proved this assignment erroneous (see O'Keefe, 2004, for a discussion of the complex taxonomic issues involved). The basicranium of this taxon is among the most primitive of all known plesiosaurs and is therefore important for documenting the condition from which later taxa are derived.

Description

The taxa *Eurycleidus* (*sensu stricto*) and *Thalassiodracon* are very similar in most aspects of the braincase and are discussed together here; *Plesiopterys* is discussed separately.

Palate and Context. In ventral view, the palate of *Thalassiodracon* is planar, lacking pterygoid flanges or other excrescences projecting ventrally from the plane of the palate, and is similar to the palate in nothosauroids. The palate is dominated by the pterygoids; these bones have a long suture on the midline stretching from the vomers anteriorly to the parasphenoid posteriorly (figs. 12.2, 12.3). This suture is broken by a small anterior interpterygoid vacuity, but behind the vacuity the pterygoids meet again, obscuring the cultriform process of the parasphenoid. This condition is again similar to the nothosauroid configuration and differs from the broadly open palate of *Araeoscelis.* (The genus *Plesiosaurus* is more derived compared with nothosauroids. In this genus, the palate is

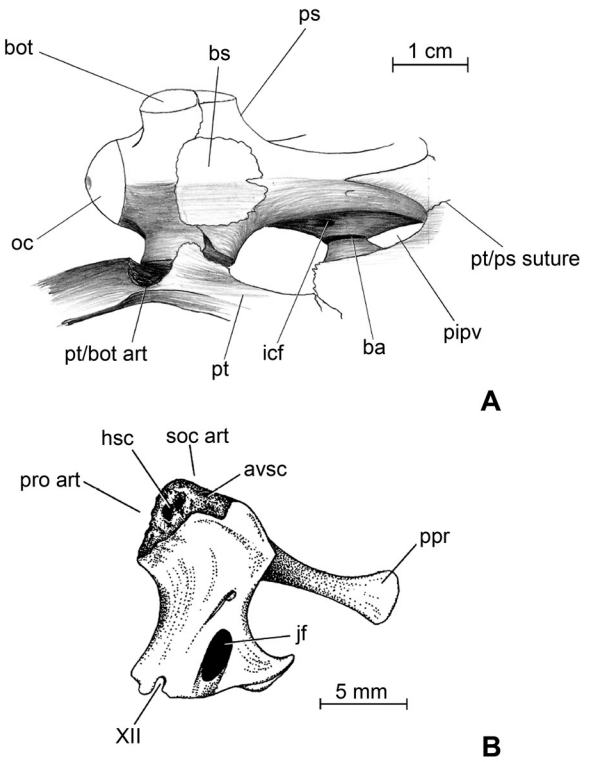

Figure 12.2. (A) Basicranium of *Thalassiodracon hawkinsi,* CAMSM J.46986. (B) Right exoccipital-opisthotic of same in oblique medial view, modified from Storrs and Taylor (1996). Abbreviations as in figure 12.1, and XII, foramen for cranial nerve XII; avsc, anterior vertical semicircular canal; hsc, horizontal semicircular canal; jf, jugular foramen; pipv, posterior interpterygoid vacuity; ppr, paraoccipital process; pro art, prootic articulation; pt, pterygoid; soc art, supraoccipital articulation.

more open and similar to the condition in *Araeoscelis;* Storrs, 1997). Farther posteriorly, the pterygoids separate and form the lateral borders of the posterior interpterygoid vacuities, participate in a broad articulation with the basioccipital tubera, and then continue laterally as the quadrate flanges of the pterygoids (fig. 12.2). Just anterior to the posterior interpterygoid vacuities, a triangular portion of the parasphenoid is exposed on the palate surface, where it sutures with the pterygoids. The posterior interpterygoid vacuities are large fenestrae affording an unobstructed view of the basicranium similar to the condition in *Araeoscelis.* The pterygoids do not meet in a midline suture behind the posterior interpterygoid vacuities in *Thalassiodracon.*

Basicranium. The basicrania of *Thalassiodracon* and *Eurycleidus* are surprisingly plesiomorphic and are best understood by comparison with the basicranium in *Araeoscelis* (fig. 12.1). In *Araeoscelis* (and *Petrolacosaurus;* Reisz, 1981), the parasphenoid is a triangular structure with a narrow cultriform process projecting anteriorly on the midline. Posteriorly, the parasphenoid broadens into a triangular sheet of bone covering the basicranium, with the two lateral cristae ventrolaterales (Reisz, 1981)

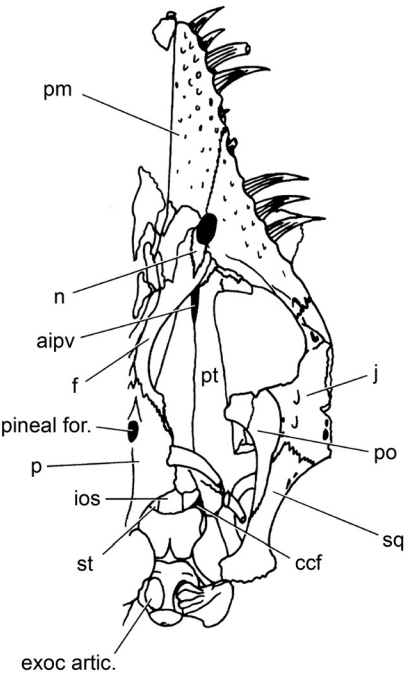

Figure 12.3. Skull of *Thalassiodracon hawkinsi* in dorsal view, OUM J. 10337. Abbreviations as in figure 12.2, and aipv, anterior interpterygoid vacuity; ccf, cerebral carotid foramen; exoc artic, exoccipital articulation; f, frontal; for, foramen; ios, interorbital septum; j, jugal; n, nasal; p, parietal; pm, premaxilla; po, postorbital; sq, squamosal; st, sella turcica. Skull length 18 cm.

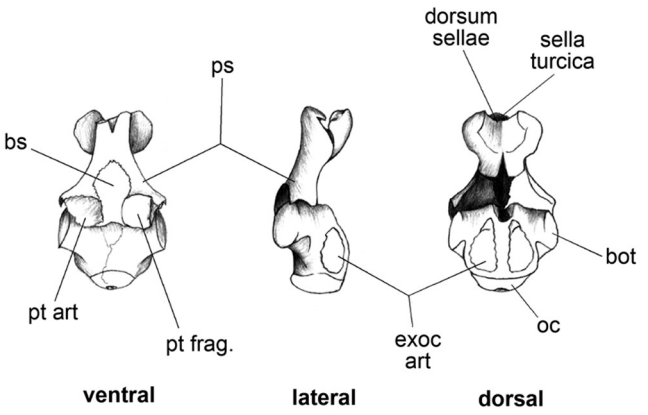

Figure 12.4. Braincase of *Eurycleidus arcuatus,* OXFUM J. 28585. Abbreviations as in figures 12.1–12.3, and frag, fragment. Fragment length 4.5 cm.

separated by a deep basisphenoid fossa on the midline. The parasphenoid has prominent articulations with the basioccipital tubera laterally but does not reach to the margin of the occipital condyle on the midline. Two small excavations in the posterior edge of the parasphenoid expose a small portion of the body of the basioccipital near the midline, but the suture between basioccipital and basisphenoid is covered by the parasphenoid. More anteriorly, the basipterygoid processes of the basisphenoid are visible on either side of the cultriform process of the parasphenoid. A groove runs around the anterior aspect of each basipterygoid process and probably carried the internal carotid artery into the floor of the hypophyseal fossa.

In *Thalassiodracon* and *Eurycleidus,* the parasphenoid is also triangular in outline (figs. 12.2, 12.4). The anterior cultriform process is obscured by the midline suture of the pterygoids (but is present in *Plesiosaurus;* O'Keefe, 2001); posteriorly, the bone expands laterally into cristae ventrolaterales that articulate with the basioccipital tubera. The parasphenoid wraps around the basioccipital tubera and participates in the articulation with the pterygoid. The basisphenoid fossa is very shallow, however, and the parasphenoid extends posteriorly for only a short distance on the midline, exposing the suture between basisphenoid and basioccipital. This suture is complex, with a slip of bone reaching posteriorly from the body of the basisphenoid and coursing ventral to the body of the basioccipital. Dorsal to the parasphenoid, the body of the basisphenoid is visible, displaying a prominent basal articulation composed of a shallow basipterygoid process and a deeper process of the pterygoid. A large foramen for the internal carotid artery is present in the body of the basisphenoid posterior to the basal articulation, in contrast to the location of this structure in *Araeoscelis.*

The lateral and dorsal aspects of the basicranium are illustrated best in the isolated braincase of the *Eurycleidus* specimen (fig. 12.4). In lateral view, the basioccipital tubera are prominent structures projecting ventrolaterally from the body of the basioccipital, and their distal ends are wrapped by the posterior margin of the parasphenoid. The articulations for the exoccipitals are clearly delineated, rugose ovoids on the dorsal surface of the basioccipital. The occipital condyle is rather poorly developed. It is a shallow dome with no groove between the condyle and the body of the basioccipital (*Thalassiodracon* and *Plesiosaurus* display a similar condition; O'Keefe, 2001). A notochordal pit is present in *Eurycleidus* and is often present in other plesiosaurs, although its presence varies ontogenetically. The anterior face of the basioccipital carries a deep fossa or notch; its position in the anterior edge of the basioccipital presumably indicates it was overlain by the medulla oblongata (Romer, 1956), although there are no obvious soft tissue structures that might be associated with this notch.

The basisphenoid does not articulate directly with the basioccipital in either *Eurycleidus* (fig. 12.4) or *Thalassiodracon* (fig. 12.2). The only contact between these two bones is formed by the ventroposterior process of the basisphenoid exposed on the palate surface (described above); hence there is a gap in dorsal view between the bodies of the basioccipital and the basisphenoid, floored by the ventrolateral basisphenoid process on the midline and the dorsal surface of the parasphenoid laterally. This condition contrasts that in nothosauroids, where the basisphenoid and basioccipital bodies have a tight, broad connection (Rieppel, 1994). *Thalassiodracon* and *Eurycleidus* also posses a deep notch in the back of the clivus, a trait they share with the pistosauroid *Cymatosaurus. Cymatosaurus* also might lack a tight connection between the bodies of the basisphenoid and basioccipital, although the basioccipital is not preserved in the one skull of *Cymatosaurus* that visibly preserves this area (Rieppel & Werneburg, 1998; see also Rieppel, 1997, 2000). If this character can be demonstrated, it will provide another link between the Plesiosauria and pistosauroids; the notch in the clivus mentioned above certainly does link these taxa.

The clivus terminates anteriorly in the dorsum sellae, a poorly developed structure in plesiosaurs consisting of the posterior wall of the sella turcica, without an obvious raised ridge as seen in *Captorhinus* (Price, 1935). The foramina for the cerebral carotid arteries are not preserved in *Eurycleidus* and probably were not ossified (they may be represented by shallow grooves in the lateral edges of the body of the basisphenoid); the foramina are large in *Thalassiodracon* (fig. 12.2). The cerebral carotids

entered the floor of the hypophyseal fossa through paired posterolateral foramina (fig. 12.3). The hypophyseal fossa itself is open laterally and anteriorly. A broad, low ridge extends forward from the back of the hypophyseal fossa on the midline and seems to have been confluent with the interorbital septum, similar to the condition seen in nothosauroids (Rieppel, 1994) and *Cymatosaurus* (Rieppel & Werneburg, 1998). The body of the basisphenoid lacks ossified clinoid processes in *Eurycleidus* and *Thalassiodracon,* although the elasmosaur *Libonectes* does have stubby ossifications in this area (Carpenter, 1997). The basipterygoid process is ossified but shallow in *Thalassiodracon,* whereas in *Eurycleidus* no distinct process has ossified.

Dorsal Braincase Ossifications (*Exoccipital, Supraoccipital, Opisthotic, Prootic*). The exoccipital and supraoccipital in stratigraphically early and morphologically primitive plesiosaurs are illustrated here by disarticulated, well-preserved elements of *Plesiopterys* (fig. 12.5) and by elements from *Thalassiodracon* (fig. 12.2). The form of the exoccipitals is very similar to that described in more derived plesiosaurs (see above), although the elements are more gracile and poorly ossified (for the following discussion see also Storrs & Taylor, 1996). In *Thalassiodracon,* the paroccipital process is narrow medially and flares laterally into an articular process for the squamosal. This process meets the body of the exoccipital near its dorsal margin. The medial surface of the exoccipital anterior to the foramen

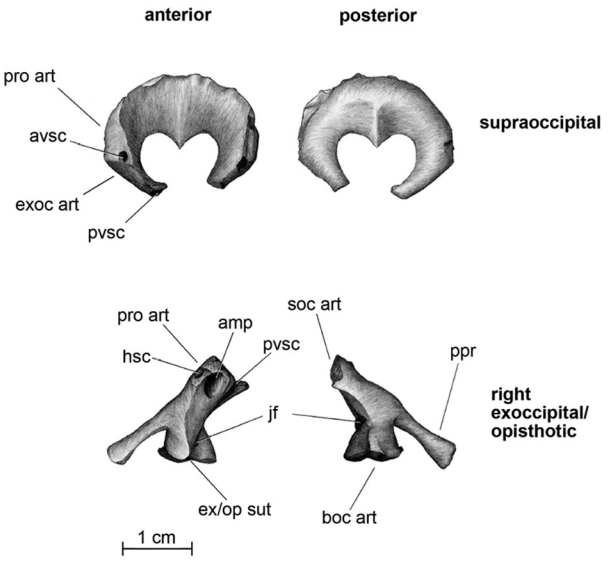

Figure 12.5. Dorsal braincase elements from *Plesiopterys,* SMNS 16812. Abbreviations as in figures 12.1–12.3, and amp, ampulla; bo, basioccipital; ex/op sut, exoccipital/opisthotic suture; pvsc, posterior vertical semicircular canal.

magnum is pierced by a prominent jugular foramen, and passage of the hypoglossal nerve is restricted to a notch at the inferior margin of this bone. The fossa for the posterior ampulla, generally open in plesiosaurs, seems to be closed over except for a fissure above the jugular foramen in *Thalassiodracon.* The suture between exoccipital and opisthotic ossifications is not visible.

The exoccipital of *Plesiopterys* (fig. 12.5) is similar, except that the fossa for the posterior ampulla is open. A foramen for the passage of the horizontal semicircular canal is present on the articular surface for the prootic in both *Plesiopterys* and *Thalassiodracon,* whereas in *Plesiopterys* a grove for the posterior vertical semicircular canal enters into the articular surface for the supraoccipital. Unlike *Thalassiodracon* and like *Peloneustes* (Andrews, 1913), the suture between the opisthotic and exoccipital ossifications is visible in *Plesiopterys,* and this suture contains the jugular foramen. The opisthotic is very similar to that in *Peloneustes,* forming the paroccipital process as well as the anterodorsal portion of the "exoccipital pillar" lateral to the foramen magnum. Also like *Peloneustes* (and *Captorhinus;* Price, 1935), the opisthotic ossification contains a fossa for the posterior ampulla and associated foramina for semicircular canals.

The supraoccipital of *Plesiopterys* is typical of those found in most early Jurassic plesiosaurs (fig. 12.5; O'Keefe, 2001, for *Plesiosaurus*). The bone is shallow anteroposteriorly, with a poorly developed articulation for the parietals on its dorsal margin. Distinct articulations for the exoccipitals and prootics are evident on the anterolateral edge. The prootic articulation is perforated by a foramen for the anterior vertical semicircular canal, and the exoccipital articulation carries a groove for the posterior vertical semicircular canal. The superior edge of the foramen magnum is divided by a prominent, pointed process surmounted by a low ridge on its posterior surface.

The prootic is a dish-shaped, quadrangular bone not exposed in the *Thalassiodracon* material and poorly preserved in *Plesiopterys* (fig. 12.6). In *Plesiopterys,* the prootics are crushed ventrally and anteriorly to their articulations with the body of the basisphenoid; they now reside anterior to the presumed position of the clinoid processes, and their articulations are posterior to this position (fig. 12.6). Both prootics seem to be lying on their medial faces, and little detailed morphology is visible. The ear remains a poorly known region in plesiosaurs. Carpenter (1997) illustrates a large fenestra ovalis bordered by the exoccipital column posteriorly, the prootic anteriorly, and the basisphenoid ventrally in the elasmosaur *Libonectes.* Most plesiosaurs represented by adequate material do have this

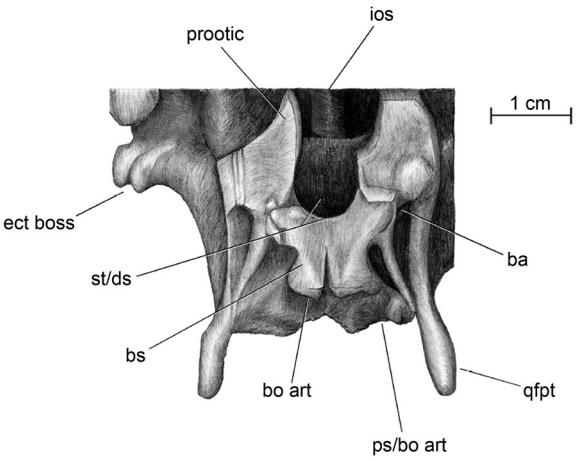

Figure 12.6. Dorsal view of basicranium from *Plesiopterys,* SMNS 16812. Abbreviations as in figures 12.1–12.3, and ds, dorsum sellae; ect, ectopterygoid; qfpt, quadrate flange of the pterygoid.

gap in the lateral braincase wall, although there is some doubt about its homology with the fenestra ovalis. Storrs and Taylor (1996) maintained that the fenestra ovalis is absent in *Thalassiodracon.* The specimen discussed by those authors and in this paper possesses a well-preserved stapes. Storrs and Taylor believed that this element articulated tightly with the body of the exoccipital; the present author could not determine whether the present location of the stapes was in fact an articulation or an artifact of preservation. Considering the development of the otic capsule in squamates (de Beer, 1937), the fenestra ovalis should pierce the lateral wall of the otic capsule in the embryo and persist between the two ossifications derived from the otic capsule in adults (prootic and opisthotic). The opisthotic is reduced in plesiosaurs and has no suture with the prootic; however, the position of the gap in the lateral braincase wall behind the prootic and in front of the opisthotic portion of the exoccipital pillar in both *Plesiopterys* and in *Peloneustes* is consistent with the position of the fenestra ovalis. The gap in the lateral braincase wall of plesiosaurs is probably too large and irregular to represent only the fenestra ovalis; the center of the otic capsule may have failed to ossify completely in plesiosaurs and this may account for some of the difficulty in assigning the relations of the footplate of the stapes.

Discussion

In general, the braincase in plesiosaurs is quite similar to those of more basal diapsids such as *Araeoscelis* and *Petrolacosaurus* and is more similar to those taxa than to the nothosaur-grade sauropterygians from which

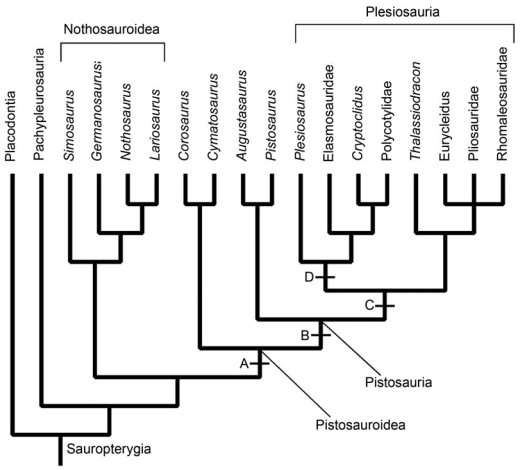

Figure 12.7. Cladogram of sauropterygian relationships, representing the combined topologies of Rieppel (2000) and O'Keefe (2001). Character changes discussed in the text occur at the following positions: A, closed occiput → open occiput; B, posterior interpterygoid vacuity closed → open; C, basal articulation obliterated → exposed, anterior interpterygoid vacuity closed → open, grooves in pterygoid for internal carotids present → absent; D, cultriform process obliterated → exposed.

plesiosaurs arose. The possibility exists that plesiosaurs arose independently from basal diapsids; however, there is excellent anatomic evidence supporting the derivation of plesiosaurs from nothosaur-grade sauropterygians, and several parsimony analyses have yielded strong support for this view (Storrs, 1991; O'Keefe, 2001; see above). Symplesiomorphy is therefore a poor explanation for the many characters that show reversals to more primitive states from the position of Nothosauroidea up to plesiosaurs (fig. 12.7). The goals of this discussion are to highlight these reversals, plot them onto the cladogram, and advance an alternative hypothesis linking the derivation of these plesiomorphic states.

The following characters are reversed to more primitive states in plesiosaurs (i.e., states present in *Araeoscelis*) relative to the conditions seen in nothosauroids (also summarized in figure 12.7):

1. The basal articulation between the pterygoids and basisphenoid is well developed in plesiosaurs and is obliterated in more basal sauropterygians.
2. Plesiosaurs do not possess well-developed grooves in the dorsal surface of the pterygoid for the passage of the internal carotid artery, unlike more basal sauropterygians.
3. The most basal plesiosaurs possess both anterior and posterior interpterygoid vacuities, whereas the palate is imperforate in nothosaur-grade sauropterygians.
4. At least some plesiosaurs have an exposed cultriform process of the parasphenoid, unlike nothosaur-grade sauropterygians.

5. The configuration of the basicranium in plesiosaurs is very similar to that in *Araeoscelis* (i.e., presence of basisphenoid fossa, cristae ventrolaterales, articulation of parasphenoid with basioccipital tubera), whereas the configuration of this region is obscured by the pterygoids in more basal sauropterygians.
6. Plesiosaurs and pistosauroids possess what Rieppel (2000) terms an "open occiput," meaning that the opisthotic is restricted to a paroccipital process, leaving the cranioquadrate passage and the posttemporal fenestra widely open. Most, but not all, nothosaur-grade sauropterygians have a closed occiput.

Of the six changes listed above, the first five are associated with the pterygoid, specifically with reduction in the extent of this bone. The sixth change, opening of the occiput, concerns reduction of the pterygoid with respect to the opening of the cranioquadrate passage but also concerns reduction of the opisthotic as well as other bones surrounding the posttemporal fenestra. Any alternative hypothesis meant to explain these six character reversals therefore should account for reduction in the pterygoid bone.

Delayed and reduced ossification in all bones of the skeleton is a well-known trend in aquatic tetrapods (Romer, 1956), and sauropterygians are no exception. Plesiosaurs are thought to have been more pelagic than more basal sauropterygians (Storrs, 1993) and show a general reduction in ossification of the postcranial skeleton (Storrs, 1991). The reduction in the pterygoid and other skull bones may be another manifestation of this trend. The pterygoid is an intramembranous bone and as such is not preformed in cartilage before ossification, as is the case in endochondral elements (Romer, 1956). However, there is still an ontogeny to the ossification of intramembranous bones; ossification begins at one or more ossification centers and spreads from these locations. Knowledge about the ontogeny of ossification of the pterygoid is available for *Lacerta* (Rieppel, 1992) and will be used as a model here.

The pterygoid is one of the first bones to ossify in the skull of *Lacerta* (and in *Podarcis;* Rieppel, 1987). Ossification begins in the middle portion of the bone close to the processus ascendens of the palatoquadrate cartilage, near the future basal articulation between basisphenoid process, the processus ascendens ossified as the epipterygoid, and possibly the pterygoid itself (Romer, 1956, 63–64). The pterygoid then ossifies quickly caudad to the quadrate portion of the palatoquadrate cartilage and forms an anterior contact with the ossifying palatine (Rieppel, 1992).

The major relations of the pterygoid therefore ossify very early in *Lacerta*—namely, the contact with the basal articulation in the center of the bone, with the quadrate via the quadrate flange and anterior and laterally with the palate surface. These contacts are correspondingly plesiomorphic and present in a wide range of reptiles and are thought to be the primitive conditions for amniotes (Romer, 1956).

Unfortunately, no information exists on skull ossification patterns in nothosaur-grade sauropterygians. However, working from the supposition that ossification of the pterygoid proceeded in the same way in these taxa as in other amniotes, the plesiomorphic contacts and relations of the pterygoid would be expected to ossify first, followed later by the conditions of the hypertrophied pterygoid that characterize nothosaur-grade sauropterygians: the closing of anterior and posterior interpterygoid vacuities and resulting obscuration of cultriform process and basicranium, obliteration of the basal articulation, and closing of the cranioquadrate passage. The closing of the cranioquadrate passage requires the presence of a foramen in the pterygoid for the passage of the internal carotid artery (present in *Simosaurus* and *Nothosaurus;* Rieppel, 1994), and the presence of bone between the occiput and basisphenoid requires a groove for the passage of the same artery. All these features might be expected to ossify later in ontogeny in accordance with von Baer's first and second laws of development (see discussion by Gould, 1977, 56). The ossification of the pterygoid around the braincase in sauropterygians may be compared with water filling a bathtub; the first water in the tub runs to the drain, the lowest point in the tub and representing the plesiomorphic contacts of the pterygoid in the analogy. As water continues to fill the tub, fenestrae in the skull are closed and structures around the braincase are enclosed: basal articulation, cultriform process, and internal carotid artery. A reduction of ossification in the plesiosaur pterygoid linked to an aquatic lifestyle would simply reverse the above process. The more derived conditions of the pterygoid would fail to ossify, leaving only the more plesiomorphic conditions in the adult. The pterygoid of adult plesiosaurs therefore would be neotenous relative to more basal sauropterygians (Gould, 1977).

The above interpretation is strongly supported by a phylogenetic argument. The reversals in the characters discussed above are plotted onto a cladogram of sauropterygian relationships in figure 12.7. If plesiosaurs had an independent derivation from basal diapsids, all these characters should reverse on the branch directly below the Plesiosauria. However, the changes are spread out over four branches, establishing a pterygoid transformation series between plesiosaurs and nothosaur-grade

sauropterygians. [Transformation series of this type also exist for several aspects of the postcranial skeleton (reviewed by O'Keefe, 2001)]. The assignment of these reversals to symplesiomorphy rather than homoplasy is therefore unlikely, and the conclusion that plesiosaurs are derived from nothosaur-grade sauropterygians seems firm. There is no clear pattern in the sequence of reversals and no ontogenetic series available for comparison with the phylogeny.

The hypothesis that the basicranium in plesiosaurs reverts to a more plesiomorphic condition due to neoteny in the ossification of the pterygoid is testable in two ways. The first is the identification and study of ontogenetic series in stem-group sauropterygians in an attempt to gather data on the ossification history of the pterygoid. Various pachypleurosaur taxa are represented by good growth series (Rieppel, 1989; Sander, 1989; O'Keefe et al., 1999), including at least one embryo. Given the early ossification of the pterygoid in *Lacerta,* however, the available material may be too late in ontogeny to offer much help. A second avenue of research would be to thin section or computerized axial tomography (CAT) scan a well-preserved nothosauroid skull. The presence and configuration of features such as the basal articulation and parasphenoid might be discernible in this way. Last, the six character state changes listed above can be accounted for by one hypothesis—reduction in ossification of the pterygoid—and so might bear consideration as a single character.

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